RECENT RESEARCH IN KOWHAI BUSH AND PROPOSALS FOR THE FUTURE

G.H. SHERLEY and J.B. CUNNINGHAM

Department of Zoology, University of Canterbury,
Christchurch, New Zealand

ABSTRACT

Hunt and Gill (1979) in their special edition of *Mauri Ora* outlined research which had been carried out in Kowhai Bush, a small, but very valuable piece of native bush several kilometers inland from Kaikoura. In particular they reviewed the extensive research which had been carried out on the rich native bird fauna and suggested future topics for research. The present paper describes the ecological studies which have been carried out on native birds in Kowhai Bush since Hunt and Gill's review. Aspects of the breeding ecology of the rifleman (*Acanthisitta chloris*) have been studied including nest building, egg laying and incubation and interactions between male and female parents. Helping (feeding of chicks by non-parent birds) appears to be important in this species. Brown creeper (*Finschia novaeseelandiae*) are present in Kowhai Bush and were the subjects of a study on bird song and dialect. Brown creeper songs with different dialects were played to resident birds within the Bush and their reactions were monitored. This bird is unusual in that interactions between male birds often consist of unison singing.

KEYWORDS: Rifleman, Brown Creeper, ecology, breeding biology, singing.

INTRODUCTION

This paper provides an update of research carried out in Kowhai Bush since Hunt and Gill's (1979) Special Publication No. 2

of *Mauri Ora* and suggests possible topics for future research.

As a Marlborough Catchment Board Flood Protection Reserve, Kowhai Bush is protected from development. The management of the Reserve is coordinated by a Scientific Advisory Committee which meets at least once a year. Its members include one person from each of the Wildlife Service, Botany Division DSIR, Department of Zoology, University of Canterbury, Ecology Division DSIR, Marlborough Catchment Board and the Soil Conservator in Kaikoura. One of the Committee's main functions is to promote research at Kowhai Bush. Thus, in the future, as in the past, researchers at Kowhai Bush can expect official support.

The physiographic characteristics of Kowhai Bush have been well described by Hunt and Gill (1979). One of the greatest assets of the bush is that it is very accessible, thus allowing research to be carried out. The forest is flat, accessible, and in many areas open and low enough to allow finding birds an easy task.

Since Gill and Hunt's description, the Kowhai Bush understorey has undergone noticeable changes. North west of the Floodway in Dobson's (1979) habitats 8 and 9 (Fig. 1), the understorey has thickened with cessation of grazing. Some of the undergrowth species concerned are *Coprosma* spp, five finger (*Pseudopanax arborea*) and wineberry (*Aristotelia serrata*). In the forest between the Floodway and Floodgate Creek there has been a similar surge of growth, but this involves the introduced montpellier broom (*Cytisus monspessulanus*) which is now very thick. However, the eastern fringe of the forest in this area (Dobson's Habitat type 1) is still relatively open underneath. The regeneration described has mostly obliterated the old tracks used by researchers in the past.

Between Floodgate Creek and the south eastern end of Kowhai Bush the understorey species is predominantly montpellier broom which has become thicker and is now encroaching into the open forest which grows on the poor stoney soils (termed habitat type 1 by Dobson). In the most southeastern area of the forest, the introduced *Clematis vitalba* has become well established and is also seen at other points in the bush. The eco-physiology of this species is currently being studied by an M.Sc. student, Judith van Gardingen from the Botany Department, University of Canterbury. The other botanical study from the Botany Department currently in progress is Linda Delph-Lively's which is investigating the evolutionary affinities of *Hebe* spp.

Two Ph.D. studies through the Zoology Department, University of Canterbury, have been completed since 1979. These have involved the brown creeper (*Finschia novaeseelandiae*) and the rifleman (*Acanthisitta chloris chloris*). Publications arising from research at Kowhai Bush since 1979 are listed in the

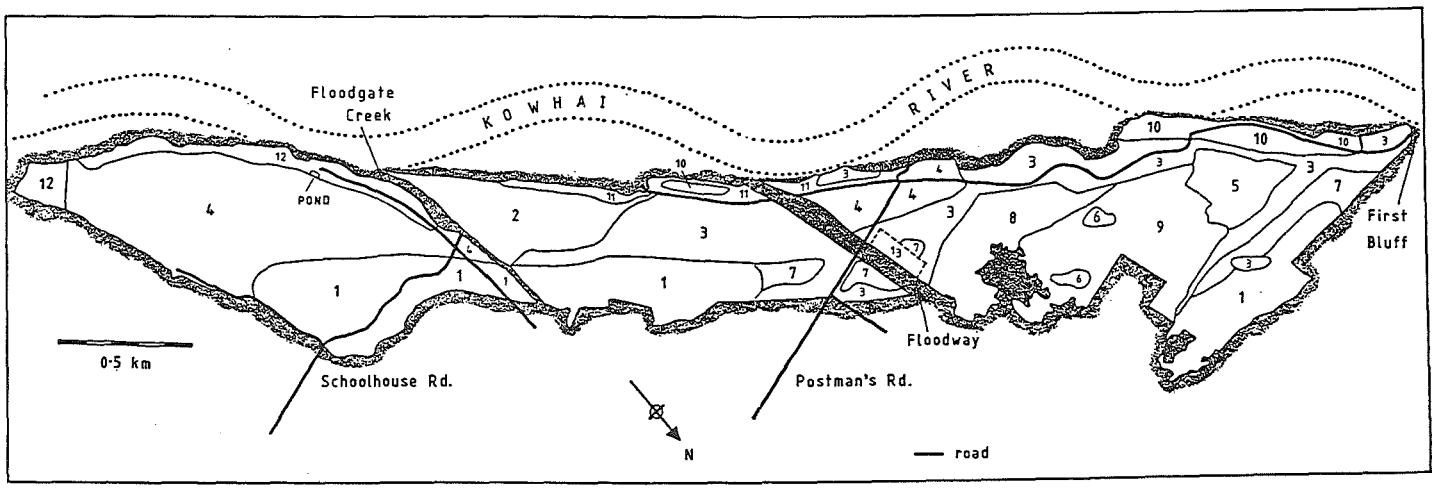

FIG.1 Map of Kowhai Bush, showing the locations of the Floodway, Floodgate Creek, and the two roads into the Bush. The numbers on the map refer to Dobson's (1979) habitats. Redrawn from Hunt and Gill (1979).

bibliography of work at Kaikoura published in this issue of *Mauri Ora*.

RESEARCH

A. RIFLEMAN (G.H. Sherley)

The South Island rifleman is the smallest bird in New Zealand along side the Grey Warbler. This study tested the hypothesis that the breeding system is highly cooperative between parents because of the need to minimise the energetic constraints of small size.

Breeding behaviour commenced with courtship feeding which began about 15 days before the first egg was laid. During this period the nest was built by both parents. Most egg laying had started by early October with oviposition occurring at 48 hour intervals. Courtship feeding continued until the last egg was laid or, if incubation was delayed after the last oviposition, until incubation commenced.

During daylight hours, most incubation was carried out by the male leaving the female with up to two hours more foraging time per day than the male. During the night the female incubated alone. The extra foraging time may have been helpful for recovery from egg-laying as each egg represented about 20% of the female's body weight and an average first clutch was 4.4 eggs. Hatching of the whole clutch was completed within 24 hours of the first egg hatching. Again, the males played the principal role in brooding and feeding of the young.

Over the four seasons from 1980 during which riflemen have been studied, 28% of first clutches and 52% of second clutches had some form of helping. Helper behaviour refers to non-parent birds involved in parental care. Helpers at first clutch nests were all unpaired males except for two instances which involved unpaired females. The relationship of first clutch helpers to the parents could not be determined except in four cases. Three of these involved the previous year's offspring helping their parents and the other a parent helping at its daughter's nest. Helpers occurring at second clutch nests were mostly juveniles of both sexes helping at their parent's nest.

Two types of helpers were identified at first and second clutch nests: "regulars" and "casuals". Regular helpers contributed to feeding of offspring significantly more than did casual helpers. Also, regular helpers aided at only one nest whereas casuals typically helped at two or more. Usually, regular helpers started between the eighth and tenth day of the

nestling period and could be seen feeding young consistently throughout the day during the nestling and post-fledgling periods. Some casual and regular male helpers paired with females from the brood which they had helped. All juvenile females and most males paired in the season in which they hatched. Pair bonds were stable and once established in a territory, pairs remained there.

During the nestling and post-fledgling periods the male parent contributed most of the food given to the young. Depending on the season's weather most pairs that raised first clutches attempted a second. Towards the end of the first clutch nestling period both parents built the second clutch nest. The extra work on the first brood performed by the male might be related to the female's production of second clutch eggs which would be laid within a week of fledging the first clutch brood. Once again, during the second clutch incubation, the male performed most of the incubation and during the nestling and post-fledgling periods the male parent contributed most towards feeding of the offspring.

The average length of incubation was 19.6 days and the nestling period 24.0 days. With egg laying and nest building included the breeding cycle (two broods) could take 104 days to complete. After the last brood of the year was fledged the annual moult began which could last into March.

The growth and development of nestling rifleman was studied to determine if "helped" nestlings fledged at a heavier weight than those that were not. There was no significant difference between young from each type of nest, though females fledged significantly heavier than did males. This pattern was apparent at the eighth day of the nestling period. Fortunately rifleman sexes could be distinguished by plumage at an early age and it was possible to determine that the primary sex ratio was unity. The rifleman breeding system thus presents a *prima facie* test case for Fisher's (1958) theory which states that parental investment per sex is equal. The functional significance of the female's retention of a larger body size (unusual in birds) might be related to meeting the demands of producing such relatively large eggs.

Riflemen did not have a song in the ordinary sense but gave a number of single note calls individually or in combination. As might be expected, riflemen did not spend any time advertising territorial boundaries by singing. In fact riflemen territories overlapped quite extensively although territorial fighting was seen between neighbouring males and females.

Like brown creepers, riflemen are gleaners and only consume invertebrates but unlike brown creepers they use the main trunks and the ground extensively while foraging. Pairs of riflemen keep in close contact with each other while foraging.

B. BROWN CREEPER (J.B. Cunningham)

A study of the brown creeper or pipipi was conducted in Kowhai Bush from 1979-1982. The species, until this investigation, was probably the least known of the native birds inhabiting New Zealand native forest. This may in part be due to the bird's cryptic colouration and habit of foraging and nesting in the canopy. Kowhai Bush was thus an ideal place to study the brown creeper because of the low canopy making observations relatively easy.

The principal aim of this study was to describe, in detail, the brown creeper's communicatory repertoire and determine the selective forces that may have shaped it. In order to accomplish this it was necessary to investigate the species' breeding ecology and its social organization during both the breeding and non-breeding seasons. Song variation within and between populations and the males' response to this variation was also examined. Finally, I attempted to understand the functional significance of a unique form of male/male vocal interaction that I have called unison singing.

BREEDING ECOLOGY

Brown creepers in Kowhai Bush have a protracted breeding season from September until February and can successfully raise two broods per year. The female builds the cup-shaped nest and incubates, but both sexes feed the young. Each egg is large and comprises ca. 18% of the female's weight. The young have a slow growth rate and when they fledge they are well developed. After leaving the nest the young spend 35-65 days with their parents before becoming independent.

Reproductive success of Kowhai Bush brown creepers was low due to predation by introduced mammals. The annual recruitment rate was also low (10-12%) whereas annual adult survival was high (ca. 81%).

The breeding strategy of this species may be adapted to the mild climatic conditions of coastal New Zealand. In these conditions competition for food and breeding sites could be high for juveniles, and parents might be under selective pressure to produce young that survive and compete successfully. Some of the species' breeding characteristics such as large eggs and long slow development may facilitate this.

SOCIAL ORGANIZATION IN THE NON-BREEDING SEASON

During the non-breeding season, members of breeding pairs remained together on their breeding territories and defended them

from other adults. Juveniles were less site specific and wandered over an area that overlapped the territories of several adult pairs. Nest siblings remained together in flocks during the winter. Flocking may increase the birds' food-finding efficiency through social facilitation or local enhancement. I feel that because brown creepers are often associated with kin, mobbing behaviour in this species could be a result of kin selection.

COMMUNICATORY BEHAVIOUR

The species' communicatory repertoire consists of 14 adult vocalizations, 5 nestling or fledgling calls and 7 non-vocal displays. Males have only one song type and they may compensate for this by singing their song in two ways. Duetting and female song may have evolved in the species because brown creepers form prolonged monogamous pair bonds and maintain territories year-round: both characteristics are also found in most duetting species. Not all of the vocal displays used by brown creepers are discrete, some were graded. Graded signals may be permitted because most interactions between individuals occur at close range, conditions under which accoustic deterioration is unlikely.

SONG DEVELOPMENT AND VARIATION

Three stages were defined in the development of male song: subsong, plastic song and full song. Young males did not learn their songs from their fathers but from neighbours with whom they vocally interacted. The sharing of songs by neighbours resulted in the formation of subdialects. Once males learned the highly stereotyped songs they showed little ability to modify them.

Song variation between five dialect populations in the Kaikoura area and three on Stewart Island were investigated. Dialects differed principally in the morphology of the notes comprising the songs and in the general pattern of the songs. Of the three hypotheses discussed by Payne (1981) to explain the origin and function of song dialects, the historical one best explains the development of the eight dialects. The differences in songs between populations may be the result of past random events and thus have no adaptive significance. However, the social adaptation hypothesis accounts for the variation of song within populations and the formation of subdialects. Males which interacted shared songs, whereas those which did not had less similar songs. The adaptive value of song sharing is discussed below.

RESPONSES OF MALES TO SONGS FROM DIFFERENT LOCALITIES

Males' responses to songs of different dialects were examined by using playback experiments. The males from two populations (Kowhai Bush and Lake Rotorua, Kaikoura) were played songs from three localities (Kowhai Bush, Lake Rotorua and West Bank of Kowhai River). Generally the birds reacted more strongly to songs from their own dialect, however, the Lake Rotorua birds responded equally to their local theme and that of the West Bank. The songs from these two dialects were qualitatively and quantitatively similar, suggesting that a male's lessened response to foreign songs is caused by physical dissimilarity to the males' own song.

NEIGHBOUR/STRANGER DISCRIMINATION AND INDIVIDUAL RECOGNITION

The ability of male brown creepers to discriminate between the songs of neighbours and strangers and their power to recognize the songs of individuals was investigated by using field playback experiments. Males responded more strongly to stranger's songs than neighbour's. The neighbours of a male in the Kowhai Bush study area which sang the Lake Rotorua theme reacted more vigorously to playback of this male's song than did non-neighbours. These results suggest that associative learning may be involved in neighbour/stranger discrimination. Furthermore, the neighbours of the male which sang the Lake Rotorua dialect made only a weak response to the song of another Lake Rotorua male. This demonstrates that males learn specific songs and are capable of individual recognition. I suggest that the terminal portion of the songs of males may be important in this recognition.

UNISON SINGING AND ITS FUNCTION IN TERRITORIAL DEFENSE

Neighbouring males temporally overlapped their songs during territorial disputes. I call this unusual vocal display "unison singing". Recordings made during unison singing bouts were analysed to determine whether or not a male adjusted his singing performance to that of the other bird. Four adjustments were sought: change in the percentage of songs overlapped, alteration in the length of the delay between the songs of the two interacting males, preference of being a leader or follower, and tendency to truncate songs during interactions. I also investigated the function of song sharing by observing the vocal interactions occurring between males which did not use the same song patterns. Males overlapped more playback songs when they were played within their territories than when they were played on territorial boundaries. No songs were overlapped when playback took place outside the territory. When two males interacted closely (0.5 m) the second male responded rapidly to the first; when further apart (2.4 m) the response was slower. Most males showed no

preference to being a leader or follower but the bird which assumed the leader role usually truncated his song towards the end of a bout. In three cases, when the leader did not curtail his song, physical fighting developed. I suggest that these adjustments are used by males to communicate intentions during territorial acquisition.

Trespassing into a neighbour's territory was common between males not sharing song patterns. Song sharing in the brown creeper may allow males to sing in unison and thus efficiently establish and maintain territorial boundaries.

C. RESEARCH TOPICS AT KOWHAI BUSH

Suggestions for further research were outlined in Gill and Hunt (1979). In addition to these we offer the following topics.

1. Rifleman

(a) Courtship feeding: The practicalities of intensively studying courtship feeding are such that almost every aspect can be tackled. Riflemen in Kowhai Bush offer an exceptional opportunity to study courtship-feeding in passerines, a group typically too difficult to follow. The past research has tackled the amount of food delivered to the female in relation to the amount of food each bird feeds themselves. A topic requiring attention is the calculation of indices of courtship feeding in relation to clutch and egg size and the onset of egglaying. This involves correlating the volume of courtship feeding occurring between a male and its mate with their egg production and date of laying. This would also test the hypothesis that courtship feeding enables birds to lay at an earlier date thus better enabling them to rear two broods in a season.

(b) Incubation: The question of whether incubation involves a nett cost to the incubating bird in terms of energy has been well debated in the literature but remains unresolved. Most studies that have addressed this question have used hole-nesting birds because nestboxes are convenient for using gas flow techniques or for setting up thermistors or heat tranducers linked up to remote recording devices. Because the birds are nesting in a box it can be conveniently checked and technical gear maintained. Much of the behavioural information is available as it has been gained in the above study. This information includes a detailed account of attentiveness for each parent day and night and other related data such as clutch size, egg size and egg weight.

(c) Cooperative Breeding: The rifleman cooperative breeding system may be considered from three points of view: (1) non-parental cooperativity (2) parental cooperativity and (3) the interrelationships of (1) and (2). Research topics occur in all

three. One of the most important questions to answer in order to theoretically explain non-parental cooperative breeding within the framework of selection theory is to establish the relationship of helpers to parents. The relationships of helpers occurring at first clutches was undetermined in almost every case in the above study. Only by colour banding over a number of seasons can relationships be determined. Banding of rifleman was carried out throughout the present study and could form a baseline for continuing work. Banding was stopped in the summer of 1983.

It appears that non-parental cooperative breeding is facultative in nature with birds opting to either help regularly and concertedly at one nest or infrequently at more than one nest. Also the incidence of each category varies from year to year. More research is needed to learn which factors determine whether a bird becomes a "regular" or "casual" helper and what factors are significant in determining the incidence of helping from year to year.

During the second clutches many offspring from the first clutch helped in a "casual" manner with their parents' second brood. Two hypotheses as to what benefits there might be for the juveniles are (i) gaining experience which will improve their own chances of breeding successfully and (ii) improving their parent's breeding success and thereby increasing their inclusive fitness. These can be tested by following the performance in their first year of breeding of "experienced" birds and by monitoring the breeding success of parents with offspring helpers.

In tackling the question as to how much cooperativity occurs between parents during the nestling and post-fledgling periods it would be advantageous to know more than simply relative feeding frequencies and a comparison of feeding quality. There could be some differences in the distance each parent flies to and from feeding stations and the time spent retrieving food items. Gaining information on the comparative foraging behaviour of parents feeding nestlings will give a more complete account of relative parental effort.

Outside of New Zealand there have been reported studies investigating the costs and benefits involved to fledged offspring of begging from parents for food as opposed to the returns from foraging for themselves. Riflemen in Kowhai Bush present an ideal opportunity to study this question to find out how the parents and the offspring optimise their returns in relation to their different requirements. For the offspring, gaining condition and a mate are important and themselves could conflict if gaining a mate involves leaving the family group. For the parents, getting rid of dependant young as soon as possible is important so that they can meet the demands of the next brood or of moulting depending on whether the first or second brood of fledglings is in

question. Yet at the same time parents must not jeopardise their breeding success by leaving young to their own devices too early. The practicalities of following family groups of rifleman and guaranteeing second clutches free from stoat (*Mustela erminea*) predation ensures the feasability of this topic.

One of the main questions that arises with the occurrence of non-parental cooperative breeding is how much do helpers help parents? The study undertaken on rifleman has tackled this by comparing parental effort between helped and non-helper first clutch nests. However, this question has not been adequately answered with respect to "regularly" helped and "casually" helped second clutch nests.

(d) Sexual dimorphism, sex ratio and parental investment: The rifleman offers an excellent opportunity to examine Fisherian theory. Some of the practical reasons for this are (i) the birds' plumage is sexually dimorphic at a very young age (ii) because nests are accessible and hence brood manipulation experiments are feasible and quantification of parental effort is easy and (iii) the risk of predation of nests is minimal.

One of the important questions in this area is whether the larger sex is really more expensive to rear than the smaller. By manipulation of brood size and sex ratio and measuring parental effort in terms of food volume delivered by parents this question may be tackled. Breeding success of experimental broods may also be documented well in Kowhai Bush because birds are relatively easy to find after fledging. For this reason, too, differential survival of the sexes may be determined. Their reproductive value may also be determined quite accurately because very few rifleman nest outside of nestboxes at Kowhai Bush.

As riflemen are sedentary and their pair bonds are stable the effect of artificially manipulated broods on a pair's future breeding performance might also be ascertained.

2. Brown Creeper

(a) Few studies have investigated the stability of song themes within dialects. By comparing the themes sung presently with those sung in the future the rate and types of changes could be determined. This would give an indication of the rate of cultural evolution occurring in isolated populations of birds.

(b) Information about the dispersal of young birds from one dialect population to another could be obtained by extensively banding young birds in each of the dialects. Later searches in each of the populations would reveal how extensive the dispersal was. Such a study would indicate how effective the barriers are between dialects.

(c) There is some evidence from this study that female brown creeper song is learned. One might expect it to vary between populations as does the song of males.

(d) If females do learn their songs, the question of who they learn it from could be answered by comparing the songs of young females with those of their mothers and neighbours which they have heard during interactions.

(e) The use of modified tape recordings of singing males could be used to determine what part(s) of the song are important in individual recognition. Indirect evidence suggests that the terminal section of the song may be the site of individual recognition.

(f) Playback of altered song could also be used to determine which characteristics of songs are important in the recognition of local dialects. This type of experiment might also reveal how different a male's song must be before it is not recognised as the song of a local male.

3. Interspecific Studies

(a) Unison singing. Unison singing as found in the brown creeper, refers to two males singing the same song at nearly the same time. This behaviour is rare among songbirds but may also occur in bellbirds (*Anthornis melanura*). Thus an investigation into the singing behaviour of this species could be rewarding. If bellbirds do perform unison singing then a comparison of this phenomenon in the brown creeper and bellbird would be interesting.

(b) Feeding ecology. Four invertebrate eating native passerines occur together in Kowhai Bush in adequate numbers for comparative research. These species are the grey warbler (*Gerygone igata*), brown creeper (*Finschia novaeseelandiae*), fantail (*Rhipidura fuliginosa*) and rifleman (*Acanthisitta chloris*). The question that arises is how do these four sympatric species partition their time and energies to avoid competing while foraging? A study area could be set up with banded territorial birds to ascertain how these species have minimised interspecific competition.

(c) Food availability. An investigation into seasonal invertebrate abundance and availability could be tied in with the above study to explain how the feeding behaviour of individual species is influenced. A study of food availability and how it affects each species at different times of the year will help to explain seasonal variations in species abundance, the chronology of breeding seasons and productivity. Distinguishing different zones for sampling invertebrates must be decided by investigating the preferred areas used by each species. This has been superficially

tackled by Gill (1980) whose study could be used to help design the research. A concurrent study of the onset of breeding for the four species would probably be needed so that observed fluctuations in food availability could be correlated with each particular seasonal pattern. This factor is significant because of the possibility of marked seasonal variation in the onset of breeding. The value of such a study cannot be over-emphasised as it is this type of information which is ultimately required by researchers to explain a species' breeding system.

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